ORIGINAL PAPER

# Nematode diversity, food web condition, and chemical and physical properties in different soil habitats of an organic farm

**Sara Sánchez-Moreno · Sean Smukler ·
Howard Ferris · Anthony T. O'Geen · Louise E. Jackson**

**Abstract** The aim of this paper was to assess biodiversity among different habitats of an organic farm and the relationships between some soil properties, nematode taxonomic diversity, and soil food web condition. Eight habitats were studied in the farm: ponds, ditches, a riparian corridor, hedgerows, and four agricultural fields (mustard, oats, fallow, and legumes). The undisturbed riparian corridor had higher soil $NO_3^- - N$ and $NH_4^+ - N$ concentrations, and potentially mineralizable N and higher abundances of bacterivore nematodes and longer food webs. Canonical correlation analysis showed associations between habitats and nematode trophic groups: predatory and bacterial-feeding nematodes in the riparian corridor and hedgerows, omnivore nematodes in the ponds and ditches, and fungal-feeding nematodes in the legume field. Soil chemical and physical properties mirrored the aboveground farm patterns and were more similar among habitats that were or had been cultivated, compared to the riparian corridor. Soil food web indices, based on functional analysis of nematode faunal composition, reflected the aboveground landscape heterogeneity. Discriminant analysis indicated that soil food web indices separated the two most disturbed habitats (ponds and tailwater ditches) from the two least disturbed habitats (the riparian corridor and hedgerows). The indices correlated with soil functioning as inferred by soil properties. Abundance of nematode taxa was not associated with aboveground landscape patterns. The complexity of the soil food web may have been influenced by (1) environmental factors that differed between years, (2) different time periods since disturbance in the various habitats, and (3) movement of nutrients and organisms by water flow between habitats in the farmscale.

**Keywords** Nematodes · Farmscale · Soil food web · Diversity · Organic farm

S. Sánchez-Moreno · H. Ferris
Department of Nematology, University of California Davis,
Davis, CA 95616, USA

S. Smukler · A. T. O'Geen · L. E. Jackson
Department of Land, Air, and Water Resources,
University of California Davis,
Davis, CA 95616, USA

S. Sánchez-Moreno (✉)
Departamento de Protección Vegetal, Instituto Nacional de
Investigación y Tecnología Agraria y Alimentaria,
28040 Madrid, Spain
e-mail: sarasm@inia.es

## Introduction

Organic farming often increases diversity and/or abundance of crops, birds, insects, plants, soil organisms, types of labor, and soil fertility and decreases the need for fertilizers and energy inputs (Van Manvstel et al. 1998; Mäder et al. 2002; Bengtsson et al. 2005; Fuller et al. 2005; Smukler et al. 2007). Organic farming typically add large amounts of organic matter and/or soil amendments, which, in turn, increase the biological activity of the soil (Mäder et al. 2002; Burger and Jackson 2003).

Nematodes are among the most diverse of soil animals, usually the most abundant of the soil metazoans and the most important secondary consumers within the soil mesofauna (Mulder et al. 2005). Nematodes have been used extensively as indicators of soil diversity and functioning (Neher 2001; Mulder et al. 2005), and there is abundant literature dealing with the nematode fauna as soil

health indicators in different farming and natural systems. However, few studies have focused on landscape distribution patterns of the nematode fauna because most of the studies relating nematode faunal composition with soil management have been carried out in homogeneous plots or single crop farms (Wardle et al. 1995; Okada and Ferris 2001; Ferris and Matute 2003; Berkelmans et al. 2003). Therefore, there is a lack of experimental and field information about how nematode populations are spatially distributed in response to both management practices and landscape heterogeneity.

The range and magnitude of soil functions are strongly related to soil biodiversity (Hunt and Wall 2002; Fitter et al. 2005). Nematodes, protozoa, microbes, earthworms, and arthropods drive such soil functions as nutrient mineralization, and the soil fauna can be responsible for up to 80% of the total nitrogen mineralization in arable soils (Didden et al. 1994). For example, greater abundance of bacterivore and fungivore nematodes increases the amount of N available to the crop (Ferris et al. 2004). Nematode trophic groups respond differently to different environmental conditions and management practices; microbivorous nematodes respond readily to changes in abundance of their food sources (Zelenev et al. 2004) and are usually highly abundant in organic fields due to higher inputs of organic matter (Yeates et al. 1997). Predatory and omnivore nematodes are more abundant in natural areas than in arable fields due to their greater sensitivity to soil disturbance (Neher 2001).

Soil biodiversity can be assessed by methods such as isolation and assessment of different organism types and measurements of biochemical and molecular parameters (Brussaard et al. 2007). Soil food web indices, based on the abundances of nematode functional guilds (nematodes with different trophic habits and life history traits), have been used to study the effect of pollution, management, and vegetation on agroecosystems (Liang et al. 2005; Stirling and Lodge 2005; Wang et al. 2006).

Chemical and physical soil properties both determine and reflect the activity of living organisms in the soil. How soil chemical, physical, and biological attributes relate to soil functioning and diversity is a relevant ecological question. Eleven properties characterizing the chemical, microbial, and physical soil status [electrical conductivity, pH, bulk density, phospholipid fatty acids (PLFA), microbial biomass carbon (MBC) potentially mineralizable nitrogen (PMN), total carbon and nitrogen, phosphorous, ammonium, and nitrate] were chosen to infer soil functioning and to relate it to soil diversity. In other studies, these properties have been well correlated with both changes in landscape management and biological community structure (Ferris and Matute 2003; Steenwerth et al. 2003).

At the farmscale level, our hypotheses were (a) heterogeneous landscapes positively affect nematode faunal diversity patterns, (b) soil chemical, microbiological, and physical properties are correlated with nematode diversity patterns and with the distribution and diversity of other organisms, and (c) nematode faunal composition is strongly related with farmscape diversity and differs among habitat types within a landscape. Thus, the objectives of this study were to: (1) assess distribution patterns of nematode populations at a landscape scale, (2) evaluate the effect of farmscale heterogeneity on soil physical, chemical, and microbiological properties, nematode activity, nematode faunal composition, and food webs of the soil to determine whether these features reflect farmscape patterns in discontinuous patches, and (3) determine nematode faunal diversity in different habitats and assess its relationship to landscape and farm management diversity.

## Materials and methods

### Study area

The study site is an organic farm located near Winters, CA, USA, and the soil is described as a fine-silty, mixed, superactive, thermic Typic Haploxeralfs (Tehama silt loam; USDA-SCS 1972). To verify the soil survey classification (USDA-SCS 1972), which indicated that the selected habitats were all on a single soil type, soil pits were excavated in all habitats (two in each of the agricultural fields) and characterized in the spring of 2005. Genetic horizons were sampled for texture and total soil C and N. After the laboratory analyses were complete, the soils were classified (Soil Survey Staff 2006). All habitats occurred on an old alluvial fan dissected by an incised intermittent stream (riparian corridor habitat), which, because of its depth in the deposited plateau, had relatively little effect on soil formation. Sedimentation from flooding is limited to the stream channel because the high degree of channel incision prevents recent deposits of sediment from reaching the study site on the dissected fan. Thus, soil forming factors at the site were fairly similar and dominated by human management. All soils were classified as from the same sub (Typic Haploxeralfs), with the exception of the pond (Aquic Haploxeralfs). The pond was somewhat distinct from the other habitats due to its seasonal inundation and excavation.

All the habitats of the farm, including the two arable fields, were included in this study. In the spring of 2005, Arcview (ESRI 2005) was used to create a stratified random sampling scheme for each of six habitat polygons: (a) ditches, which surround the arable fields, (b) irrigation tailwater ponds, which collected water runoff from the

fields, (c) north field of oats, (d) south field of tomato (separated from the north field by a country road), (e) hedgerows, composed of perennial native shrubs and herbaceous perennials in a discontinuous hedge surrounding the farm, and (f) riparian corridor, which is the south border of the farm and is composed of woody tree species, subshrubs, herbaceous perennials, and ruderal annual plants (Fig. 1). In the spring of 2006, the same methodology was used to re-randomize plots and to include additional mustard and oats cover crop treatments (riparian corridor, hedgerow, north field-mustard, north field-fallow, north field-legume, south field-oats, drainage ditches, and tailwater pond). Samples were collected at the bottom edge of the tailwater pond where it was not inundated. Using each randomized point as the center, 16 m$^2$ square plots were established for aboveground vegetation analysis (Smukler, in preparation). Within each sampling plot, four 50 cm$^2$ subplots were established in each cardinal direction at random distances from the plot center. Samples were taken at 0–15 and 15–30 cm depths from the center of the four 50 cm$^2$ sub-plots, composited by depth and mixed in the field before storage in coolers for transportation back to the laboratory. For bulk density measurements, soil pits were excavated within each sampling plot and brass rings (8.5 cm diameter×6 cm deep) were pounded into the side of the pit at 0–6, 8–15, 16–22, and 23–30 cm depths then excavated and dried at 105°C. Soil samples were collected in March 2005 and 2006, before cover crops were chopped and incorporated into the soil.

Soil properties

Fresh soil samples were stored on ice and transported to the laboratory where they were homogenized, subsampled, and then analyzed for gravimetric soil moisture content, KCl-extractable $NO_3^- - N$ and $NH_4^+ - N$ colorimetrically (Miranda et al. 2001), nematodes, and PLFA (Bossio and Scow 1995). A 7-day anaerobic incubation was used to determine potentially mineralizable N (Waring and Bremner 1964). MBC was measured by the fumigation extraction method (Vance et al. 1987). The remaining sample was air dried and used later for analysis of electrical conductivity (EC; Rhoades 1982) and pH (US Salinity Laboratory 1954). Air dried samples were analyzed for total N and C by the combustion gas analyzer method (Pella 1990) and Olsen P (Olsen and Sommers 1982) at the Division of Agriculture and Natural Resources Analytical Laboratory at the University of California at Davis. Data for $NH_4^+ - N$ and $NO_3^- - N$ are expressed both in µg/g dry soil and kg/m$^2$. Data for total soil C and N are expressed both in soil percentage and kg/m$^2$. Bulk density was calculated from the dry mass of soil per volume collected in a brass ring and averaged for the 0–15 and 15–30 cm depths.

Nematode sampling and identification

Nematodes were extracted using a modification of the sieving and Baermann funnel method (Barker 1985). In 2005, nematodes were extracted from 100 g of soil, and to
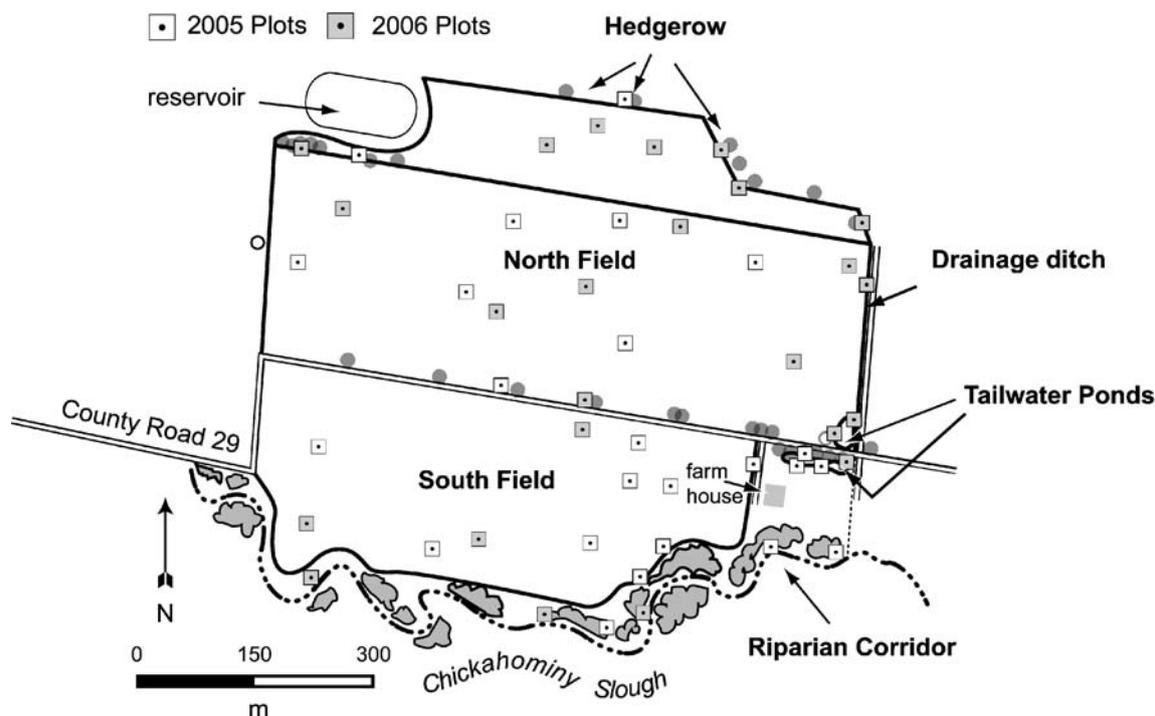


Fig. 1 Farm map including the habitats sampled in 2005 and 2006

improve nematode recovery, nematodes were extracted from 250 g in 2006; nematode counts were expressed as number of nematodes per 100 g soil.

The total number of nematodes was counted in each sample at ×50 magnification, and the first 200 individuals were identified to genus/family level. Nematode taxa were assigned to trophic groups (Yeates et al. 1993) and functional guilds (Bongers and Bongers 1998). Shannon's (1948) and Simpson's (1949) diversity indices were calculated, and soil food web indices (Ferris et al. 2001) were used to assess soil food web status. Given the uncertain trophic habit of the nematodes in the family Tylenchidae, half of the nematodes on such taxa were considered fungal-feeders and half plant-feeders.

Statistical analysis

Kruskall–Wallis analysis of variance (ANOVA) was used to detect significant differences in abundance of nematode taxa, nematode diversity, soil food web indices, and soil properties between habitats. The Mann–Whitney test was applied post-hoc. Spearman rank-order correlation coefficients were used to detect significant relationships between continuous variables.

Three functional categories were used to assess relationships between the farmscale and soil diversity and functioning. The first category is comprised of soil biotic and abiotic properties [N, C, $NH_4^+ - N$, $NO_3^- - N$, PMN, bulk density (BD), pH, soil moisture, electrical conductivity (EC), MBC and phosphorus], all of which are strongly related to soil physical and chemical characteristics and microbial activity. The second category is comprised of abundance of different nematode taxa. The abundance of nematode taxa not only depends on soil properties but also on population dynamics, food availability, and interactions with other organisms. Nematode taxa abundances were expressed as absolute abundance (number of nematodes in taxon $i$ per 100 g of fresh soil) and as relative abundance (number of nematodes in taxon $i$/total number of nematodes in the sample per 100 g of fresh soil). The last category describes the condition of the soil food web, inferred from soil food web indices [Structure Index (SI), Enrichment Index (EI), Channel Index (CI) and Basal Index (BI)]. These indices assess overall soil trophic relationships, soil food web connectance, organic matter decomposition pathways, and effects of perturbations on the soil food web (Ferris et al. 2001).

Univariate analyses were performed for comparing nematode community composition, soil food web condition, and soil properties among different habitats in 2005 and 2006. Multivariate analyses used to infer relationships between nematodes, landscape, and soil properties were only performed with 2006 data. Canonical correspondence analysis (CCA) was used to detect and summarize relationships between trophic group abundances, soil properties, and nature of the habitat. The results of the CCA can be represented as a bidimensional plot in which physical gradients are revealed and relationships between variables can be inferred. Variables positioned in close proximity on the graph are more closely related. The procedure allows detection of complex patterns and associations among variables.

Discriminant analysis was applied to three data categories: (a) soil chemical and biochemical properties, (b) absolute abundance of nematode taxa, and (c) soil food web indices. Significant variables in the model were selected by forward stepwise regression. Wilks' Lambda values are used to denote the statistical significance of the discriminatory power of the models, ranging from 1.0 (no discriminatory power) to 0.0 (perfect discriminatory power).

For cluster analyses of the three data categories, Squared Mahalanobis Distance matrices were used to infer the degree of similarity among habitats in terms of their nematode faunal composition, soil food web condition, and soil properties. Euclidean distances were used to construct cluster charts that summarize similarity relationships between sample groups from different habitats.

All the analyses were performed using the Statistica software package (StatSoft 1996).

## Results

Nematode faunal composition

Thirty-three nematode taxa were identified in 2005 and 35 in 2006. In 2005, four nematode taxa were significantly different in abundance among habitats (Table 1), and one nematode taxon, a species in the family Hoplolaimidae, was found in only one habitat, the riparian corridor. In 2006, five nematodes presented significant different abundances among habitats, and nine genera appeared in only one habitat (Table 1).

Nematode functional diversity and soil food webs

In 2005, three trophic groups differed in abundance among habitats (Table 2). Relative abundances of herbivores and predators were higher in the riparian corridor than in ponds and the south field at 0–15 and 15–30 cm, respectively. Absolute abundances of fungal-feeders were greatest in the hedgerows and in both fields at 0–15 cm. The total number of nematodes, the SI, and the Shannon's diversity index also showed some significant differences among habitats.

**Table 1** Average number of nematodes/100 g soil (±SE) in each habitat in 2005 and 2006 (average 0–30 cm depth)

| | | 2005 | | | | | | 2006 | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Taxon | Group | Pond | Ditch | N field | S field | Hedge | Riparian | Pond | Ditch | Legume | Fallow | Mustard | Oats | Hedge | Riparian |
| Mesorhabditis | Ba-1 | 45.32 | 20.62 | 61.81 | 54.09 | 44.41 | 16.20 | 1.23a | 7.11ab | 2.64ab | 10.00ab | 0.64a | 7.53ab | 23.30b | 14.77ab |
| | | ±36.42 | ±10.89 | ±17.70 | ±7.50 | ±23.20 | ±10.62 | ±0.42 | ±2.85 | ±1.64 | ±6.42 | ±0.33 | ±5.38 | ±7.39 | ±4.42 |
| Panagrolaimus | Ba-1 | 1.69 | 2.68 | 26.00 | 7.24 | 8.74 | 18.74 | 3.47 | 4.85 | 4.79 | 8.57 | 27.82 | 4.86 | 5.11 | 14.28 |
| | | ±1.34 | ±1.34 | ±12.13 | ±2.38 | ±4.92 | ±13.19 | ±1.64 | ±2.61 | ±0.50 | ±6.14 | ±17.51 | ±2.61 | ±0.96 | ±3.01 |
| Eumonhystera | Ba-1 | 1.65 | 0.00 | 2.51 | 3.00 | 3.89 | 2.65 | 0.09 | 0.26 | 2.99 | 5.56 | 0.31 | 0.75 | 3.48 | 1.21 |
| | | ±1.65 | ±0.00 | ±1.53 | ±1.29 | ±2.50 | ±1.33 | ±0.09 | ±0.13 | ±0.57 | ±2.51 | ±0.31 | ±0.75 | ±1.66 | ±0.31 |
| Dauerlarva | (Ba-1) | 0.00 | 0.30 | 1.20 | 0.43 | 5.57 | 0.98 | 0.47 | 0.42 | 0.00 | 0.00 | 0.14 | 0.34 | 11.44 | 0.44 |
| | | ±0.00 | ±0.30 | ±0.75 | ±0.43 | ±4.78 | ±0.62 | ±0.47 | ±0.42 | ±0.00 | ±0.00 | ±0.14 | ±0.34 | ±8.45 | ±0.27 |
| Cruznema | Ba-1 | 0.32 | 0.00 | 4.64 | 0.00 | 0.55 | 8.51 | 0.75 | 5.97 | 23.59 | 45.16 | 41.79 | 11.81 | 2.40 | 1.73 |
| | | ±0.32 | ±0.00 | ±3.43 | ±0.00 | ±0.55 | ±8.51 | ±0.42 | ±3.36 | ±7.13 | ±14.82 | ±28.10 | ±6.55 | ±2.40 | ±1.63 |
| Rhabditidae | Ba-1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00a | 0.42ab | 0.00a | 0.00ab | 0.00a | 6.48b | 0.00a | 0.00a |
| | | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.42 | ±0.00 | ±0.00 | ±0.00 | ±3.61 | ±0.00 | ±0.00 |
| Acrobeles | Ba-2 | 0.00 | 0.00 | 0.00 | 0.69 | 0.00 | 0.34 | 0.13 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.20 |
| | | ±0.00 | ±0.00 | ±0.00 | ±0.69 | ±0.00 | ±0.34 | ±0.07 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.20 |
| Acrobeloides | Ba-2 | 58.19 | 64.62 | 129.00 | 229.90 | 95.56 | 83.66 | 7.73a | 52.58ab | 32.68ab | 55.94ab | 45.36ab | 66.56b | 22.67ab | 18.86ab |
| | | ±17.95 | ±24.27 | ±45.73 | ±44.34 | ±15.96 | ±35.61 | ±3.53 | ±24.18 | ±5.18 | ±5.86 | ±10.91 | ±7.98 | ±6.14 | ±1.39 |
| Plectus | Ba-2 | 1.65 | 2.27 | 6.90 | 3.77 | 3.31 | 3.57 | 1.64 | 0.13 | 7.05 | 8.35 | 2.62 | 6.06 | 1.96 | 1.92 |
| | | ±1.20 | ±1.15 | ±2.56 | ±1.45 | ±1.79 | ±0.56 | ±0.62 | ±0.13 | ±2.72 | ±6.34 | ±0.60 | ±1.47 | ±1.06 | ±0.64 |
| Cephalobidae | Ba-2 | 2.33 | 28.31 | 18.15 | 10.37 | 20.98 | 17.45 | 3.36 | 5.16 | 5.70 | 9.87 | 17.65 | 14.01 | 6.91 | 0.53 |
| | | ±2.33 | ±26.59 | ±7.14 | ±3.15 | ±6.34 | ±10.87 | ±2.42 | ±3.12 | ±5.41 | ±4.52 | ±6.29 | ±6.83 | ±3.84 | ±0.15 |
| Metacrolobus | Ba-2 | 1.48 | 0.52 | 0.13 | 1.65 | 1.03 | 0.84 | 0.00 | 0.40 | 0.00 | 0.00 | 0.31 | 0.35 | 0.17 | 0.56 |
| | | ±1.48 | ±0.52 | ±0.13 | ±0.62 | ±1.03 | ±0.42 | ±0.00 | ±0.23 | ±0.00 | ±0.00 | ±0.31 | ±0.19 | ±0.17 | ±0.12 |
| Bunonema | Ba-1 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 |
| | | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.07 |
| Wilsonema | Ba-2 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.47 |
| | | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.34 |
| Prismatolaimus | Ba-3 | 0.00 | 0.39 | 2.29 | 2.22 | 2.31 | 1.83 | 0.09 | 0.07 | 0.68 | 1.76 | 0.15 | 2.63 | 2.46 | 8.42 |
| | | ±0.00 | ±0.39 | ±1.03 | ±1.07 | ±1.30 | ±1.26 | ±0.09 | ±0.07 | ±0.42 | ±1.49 | ±0.15 | ±1.32 | ±0.53 | ±5.94 |
| Achromadora | Ba-3 | 0.00 | 0.00 | 0.00 | 0.36 | 0.00 | 0.54 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| | | ±0.00 | ±0.00 | ±0.00 | ±0.36 | ±0.00 | ±0.54 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Alaimus | Ba-4 | 0.00 | 0.00 | 0.31 | 0.00 | 0.55 | 0.41 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.31 | 0.00 | 0.39 |
| | | ±0.00 | ±0.00 | ±0.31 | ±0.00 | ±0.55 | ±0.41 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.31 | ±0.00 | ±0.19 |
| Aphelenchoides | Fu-2 | 14.25 | 12.23 | 24.84 | 16.37 | 10.83 | 10.13 | 16.19 | 13.31 | 23.22 | 35.53 | 47.97 | 32.22 | 17.61 | 12.40 |
| | | ±12.31 | ±7.34 | ±9.46 | ±6.91 | ±7.69 | ±4.07 | ±13.32 | ±2.02 | ±11.85 | ±20.30 | ±21.73 | ±8.94 | ±10.46 | ±4.32 |
| Aphelenchus | Fu-2 | 8.29a | 35.90ab | 42.17a | 126.71b | 36.46ab | 10.22a | 5.66a | 90.07ab | 161.73b | 43.40a | 42.73a | 61.64ab | 10.94a | 1.45a |
| | | ±5.03 | ±20.70 | ±8.95 | ±30.74 | ±2.45 | ±4.77 | ±3.84 | ±52.98 | ±23.03 | ±15.94 | ±15.64 | ±4.64 | ±1.25 | ±0.44 |
| Ditylenchus | Fu-2 | 3.29 | 2.85 | 6.54 | 5.54 | 1.82 | 4.61 | 0.00 | 44.23 | 0.55 | 0.75 | 0.52 | 0.45 | 0.12 | 2.32 |
| | | ±2.73 | ±1.03 | ±2.07 | ±2.03 | ±1.43 | ±2.86 | ±0.00 | ±35.81 | ±0.55 | ±0.75 | ±0.52 | ±0.27 | ±0.12 | ±1.65 |
| Tylenchidae | | 100.59a | 49.98a | 139.44a | 190.93ab | 330.40b | 86.94a | 13.54 | 11.77 | 15.30 | 38.17 | 31.20 | 34.22 | 14.89 | 14.68 |

**Table 1** (continued)

| | 2005 | | | | | | 2006 | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | Pond | Ditch | N field | S field | Hedge | Riparian | Pond | Ditch | Legume | Fallow | Mustard | Oats | Hedge | Riparian |
| Fu/Pp-2 | ±47.79 | ±17.03 | ±30.97 | ±26.62 | ±95.78 | ±27.57 | ±6.07 | ±5.14 | ±2.81 | ±13.78 | ±8.08 | ±11.30 | ±4.04 | ±3.92 |
| Aprutides | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.95 | 0.00 |
| Fu-2 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.66 | ±0.00 |
| Diphtherophora | 0.39 | 0.00 | 1.25 | 0.37 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.17 | 0.00 | 0.00 |
| Fu-3 | ±0.39 | ±0.00 | ±0.72 | ±0.37 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.17 | ±0.00 | ±0.00 |
| Tylencholaimus | 1.65a | 1.49a | 0.44a | 1.33a | 42.93b | 4.46a | 0.00 | 0.00 | 1.25 | 0.38 | 17.64 | 2.35 | 6.35 | 0.08 |
| Fu-4 | ±1.20 | ±1.03 | ±0.20 | ±1.33 | ±16.13 | ±4.46 | ±0.00 | ±0.00 | ±1.25 | ±0.38 | ±17.43 | ±2.10 | ±2.20 | ±0.08 |
| Paratylenchus | 1.10 | 0.00 | 0.64 | 0.00 | 0.00 | 0.67 | 0.00 | 0.00 | 0.00 | 0.26 | 0.00 | 0.00 | 27.02 | 28.92 |
| Pp-2 | ±1.10 | ±0.00 | ±0.64 | ±0.00 | ±0.00 | ±0.67 | ±0.00 | ±0.00 | ±0.00 | ±0.26 | ±0.00 | ±0.00 | ±17.71 | ±28.78 |
| Psilenchus | 3.87 | 0.00 | 0.00 | 0.00 | 0.00 | 0.67 | 9.43 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pp-2 | ±3.87 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.67 | ±8.25 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Gracilacus | 0.00 | 1.16 | 0.00 | 0.38 | 9.63 | 3.24 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pp-2 | ±0.00 | ±1.16 | ±0.00 | ±0.38 | ±9.63 | ±2.84 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Ecphyadophora | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.07 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Fu-2 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.07 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Pratylenchus | 1.94 | 5.48 | 24.26 | 13.28 | 41.23 | 11.17 | 0.00a | 1.25ab | 0.24a | 0.78ab | 0.00a | 10.83b | 7.00ab | 1.96ab |
| Pp-3 | ±1.94 | ±4.37 | ±3.48 | ±5.78 | ±21.33 | ±3.84 | ±0.00 | ±0.77 | ±0.24 | ±0.45 | ±0.00 | ±4.86 | ±3.45 | ±0.40 |
| Tylenchorhynchus | 5.17 | 16.03 | 61.18 | 84.26 | 66.96 | 88.28 | 3.19 | 21.10 | 26.68 | 33.47 | 44.87 | 52.28 | 2.36 | 4.10 |
| Pp-3 | ±2.87 | ±5.26 | ±18.35 | ±9.87 | ±21.37 | ±46.77 | ±1.16 | ±10.58 | ±6.25 | ±15.25 | ±19.47 | ±14.97 | ±1.30 | ±1.10 |
| Helicotylenchus | 1.33 | 44.01 | 0.42 | 0.49 | 16.39 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pp-3 | ±1.33 | ±44.01 | ±0.42 | ±0.31 | ±13.28 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Hemicriconemoides | 0.00ab | 0.39ab | 0.00a | 0.36ab | 0.00ab | 2.65b | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pp-3 | ±0.00 | ±0.39 | ±0.00 | ±0.36 | ±0.00 | ±1.77 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Hoplolaimidae | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 1.23 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pp-3 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±1.23 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Meloidogyne | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.27 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| Pp-3 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.27 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Xiphinema | 0.00 | 0.39 | 0.65 | 0.00 | 2.77 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.31 | 0.29 | 0.00 |
| Pp-5 | ±0.00 | ±0.39 | ±0.44 | ±0.00 | ±2.77 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.31 | ±0.29 | ±0.00 |
| Tripyla | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.15 | 0.00 | 0.00 | 0.00 | 0.00 |
| P-3 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.15 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Qudsianematidae | 1.75 | 5.10 | 3.62 | 5.67 | 4.91 | 9.45 | 0.09 | 0.20 | 1.46 | 0.97 | 0.38 | 0.93 | 2.36 | 0.89 |
| O-4 | ±1.00 | ±3.37 | ±1.60 | ±2.67 | ±1.56 | ±4.68 | ±0.09 | ±0.11 | ±0.49 | ±0.76 | ±0.28 | ±0.93 | ±0.59 | ±0.24 |
| Mylonchulus | 1.04 | 0.00 | 0.00 | 0.36 | 0.00 | 0.67 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.14 | 0.00 | 0.00 |
| P-4 | ±0.69 | ±0.00 | ±0.00 | ±0.36 | ±0.00 | ±0.67 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.14 | ±0.00 | ±0.00 |
| Mononchus | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 | 0.12 | 0.00 | 0.00 | 0.00 | 0.00 | 0.00 |
| P-4 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.12 | ±0.00 | ±0.00 | ±0.00 | ±0.00 | ±0.00 |
| Discolaimus | 0.00 | 0.39 | 0.52 | 0.73 | 0.00 | 0.34 | 0.00 | 0.00 | 1.17 | 0.00 | 0.00 | 0.87 | 0.44 | 0.00 |
| P-5 | ±0.00 | ±0.39 | ±0.52 | ±0.62 | ±0.00 | ±0.34 | ±0.00 | ±0.00 | ±1.17 | ±0.00 | ±0.00 | ±0.44 | ±0.34 | ±0.00 |

| Aporcelaimidae O-5 | 0.00 ±0.00 | 0.00 ±0.00 | 8.89 ±6.97 | 0.63 ±0.40 | 1.90 ±1.90 | 1.05 ±0.61 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.10 ±0.10 | 0.00 ±0.00 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Dorylaimidae O-4 | 8.43 ±4.99 | 11.03 ±5.49 | 9.68 ±3.18 | 11.13 ±5.36 | 7.21 ±6.57 | 0.00 ±0.00 | 0.22 ±0.12 | 1.13 ±0.94 | 1.40 ±1.22 | 0.15 ±0.15 | 1.22 ±0.92 | 1.12 ±0.73 | 0.32 ±0.18 | 0.07 ±0.07 |

a, b Different letters mean significant differences on nematode abundances among habitats ($P<0.05$). Comparisons were done within 2005 and 2006 data independently. Trophic group of nematode taxa ($Ba$ bacterial-feeders, $Fu$ fungal-feeders, $Pp$ plant-parasites and herbivores, $P$ predators, $O$ omnivores) and colonizer-persistence group (1 to 5, Bongers and Bongers 1998) are indicated

At the second sampling (2006), absolute abundances of bacterial-feeding nematodes were higher in the oat field and the fallow than in ponds at 0–15 and 15–30 cm, respectively (Table 3). At 0–15 cm depth, bacterivore nematodes were relatively more abundant in hedgerows and the riparian corridor than in the legume field, while, on the contrary, fungal-feeders were relatively more abundant in the legume field than in the hedgerows and in the riparian area. The EI and the Simpson Index also showed some significant differences among habitats at 0–15 cm depth in 2006; the CI varied at both depths and the Shannon Index differed among habitats at 15–30 cm depth (Table 3).

Soil properties

In 2006, $NO_3^- - N$ and $NH_4^+ - N$ soil content (measured both as µg/g and kg/m$^2$), PMN, and EC were significantly higher in the riparian corridor than in any other habitat at 0–15 cm depth ($P<0.05$; Table 4). At 15–30 cm, some significant differences were also found among habitats.

Relationships between nematode community, soil properties, and farm habitats

Many bacterial-feeding taxa, including *Mesorhabditis*, *Panagrolaimus*, *Metacrolobus*, *Plectus*, *Prismatolaimus*, and *Wilsonema*, were positively correlated to at least one soil property ($NO_3^- - N$, $NH_4^+ - N$, PMN, and/or MBC; Table 5). *Cruznema* was the only bacterivore negatively correlated with $NO_3^- - N$ and $NH_4^+ - N$, as was the fungivore *Aphelenchus*. The EI, CI, and BI were generally related to total N and C contents (Table 5). Other relationships between soil properties and nematode taxa and trophic groups are shown in Table 5.

A CCA bidimensional plot of relationships among soil properties, habitats, and nematode trophic groups indicates that higher values of $NO_3^- - N$, EC, PMN, C, N, and $NH_4^+ - N$ were associated with the riparian corridor and the hedgerow area and, to a lesser extent, with the oat field (Fig. 2). Mid-range values of those properties were associated with the mustard cover crop and the fallow in the north field. Higher bulk density and soil moisture were associated with ponds and ditches. Predatory and bacterial-feeding nematodes were most highly associated with the riparian corridor, the hedgerows, and their characteristic soil properties. Fungal-feeding nematodes were mainly associated with the legume field. Omnivore nematodes were associated with ponds and ditches.

Habitat discrimination

Discriminant models were developed separately for soil properties (Category 1), abundances of nematode taxa

**Table 2** Average (±SE) relative and absolute (A) abundance of trophic groups (*Ba* bacterial-feeders, *Fu* fungal-feeders, *Pp* plant-parasites and herbivores, *P* predators, *O* omnivores), soil food web indices (*EI* Enrichment Index, *SI* Structure Index, *CI* Channel Index, *BI* Basal Index) and nematode community descriptors (*Simp* Simpson's diversity index, *Shannon* Shannon's diversity index, *N* total number of nematodes per 100 g soil, *S* taxa richness) in 2005

| | 0–15 cm | | | | | | 15–30 cm | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ditch | Pond | Hedge | Riparian | N Field | S Field | Ditch | Pond | Hedge | Riparian | N Field | S Field |
| Ba | 0.50 ±0.03 | 0.27 ±0.04 | 0.23 ±0.06 | 0.39 ±0.09 | 0.44 ±0.07 | 0.39 ±0.03 | 0.40 ±0.19 | 0.63 ±0.19 | 0.30 ±0.07 | 0.32 ±0.08 | 0.36 ±0.03 | 0.40 ±0.04 |
| Fu | 0.38 ±0.01 | 0.64 ±0.09 | 0.58 ±0.12 | 0.34 ±0.11 | 0.38 ±0.05 | 0.48 ±0.03 | 0.32 ±0.05 | 0.28 ±0.14 | 0.42 ±0.09 | 0.28 ±0.04 | 0.37 ±0.03 | 0.40 ±0.04 |
| Pp | 0.06ab ±0.02 | 0.02a ±0.02 | 0.16ab ±0.08 | 0.24b ±0.04 | 0.13ab ±0.04 | 0.11ab ±0.02 | 0.27 ±0.18 | 0.02 ±0.01 | 0.21 ±0.05 | 0.33 ±0.12 | 0.23 ±0.03 | 0.18 ±0.03 |
| P | 0.01 ±0.00 | 0.02 ±0.01 | 0.01 ±0.00 | 0.03 ±0.02 | 0.04 ±0.03 | 0.01 ±0.00 | 0.00ab ±0.00 | 0.00ab ±0.00 | 0.00ab ±0.00 | 0.01b ±0.01 | 0.00ab ±0.00 | 0.00a ±0.00 |
| O | 0.05 ±0.04 | 0.05 ±0.04 | 0.01 ±0.01 | 0.00 ±0.00 | 0.01 ±0.00 | 0.02 ±0.01 | 0.01 ±0.01 | 0.05 ±0.03 | 0.02 ±0.01 | 0.02 ±0.01 | 0.02 ±0.02 | 0.01 ±0.00 |
| Ba A | 161.20 ±82.51 | 53.09 ±15.08 | 262.07 ±77.69 | 264.66 ±116.77 | 413.90 ±100.73 | 441.37 ±116.96 | 78.20 ±43.14 | 172.18 ±85.52 | 111.75 ±21.45 | 46.79 ±17.38 | 92.00 ±14.56 | 186.05 ±24.73 |
| Fu A | 118.01a ±54.37 | 116.15a ±27.02 | 676.28b ±178.10 | 192.68a ±44.46 | 329.90ab ±63.02 | 494.06ab ±73.78 | 86.89 ±35.34 | 140.77 ±80.06 | 168.59 ±49.71 | 40.06 ±11.02 | 99.47 ±19.37 | 188.44 ±23.69 |
| Pp A | 19.69 ±11.02 | 5.96 ±5.20 | 171.60 ±72.21 | 163.08 ±67.24 | 108.75 ±35.43 | 106.35 ±20.34 | 112.89 ±98.75 | 10.92 ±6.70 | 83.07 ±24.27 | 43.57 ±21.09 | 64.27 ±17.45 | 90.43 ±18.22 |
| P A | 2.68 ±1.87 | 3.63 ±1.87 | 6.74 ±5.27 | 18.86 ±9.47 | 23.40 ±13.00 | 5.44 ±2.94 | 0.77 ±0.77 | 0.00 ±0.00 | 0.00 ±0.00 | 1.76 ±1.18 | 0.00 ±0.00 | 1.27 ±0.64 |
| O A | 16.09 ±8.06 | 9.84 ±7.63 | 13.32 ±13.32 | 0.00 ±0.00 | 14.71 ±4.52 | 23.02 ±9.94 | 1.59 ±0.80 | 20.86 ±10.47 | 8.00 ±1.68 | 2.41 ±1.22 | 7.33 ±5.59 | 7.32 ±2.01 |
| EI | 52.41 ±2.74 | 52.97 ±4.57 | 55.34 ±2.68 | 58.42 ±1.92 | 60.53 ±5.12 | 51.20 ±1.23 | 46.94 ±0.97 | 41.72 ±21.85 | 56.17 ±6.44 | 47.94 ±7.99 | 54.68 ±4.78 | 49.51 ±2.50 |
| SI | 19.32 ±11.88 | 19.31 ±11.65 | 23.03 ±4.40 | 16.33 ±10.07 | 23.72 ±8.07 | 11.62 ±3.62 | 12.95ab ±6.39 | 20.16ab ±10.52 | 45.59b ±9.80 | 18.60ab ±11.98 | 14.17ab ±7.00 | 10.99a ±2.19 |
| CI | 45.26 ±1.77 | 67.80 ±7.80 | 62.97 ±11.93 | 38.80 ±12.71 | 38.52 ±4.98 | 58.51 ±3.37 | 64.24 ±20.16 | 39.05 ±14.57 | 54.32 ±19.35 | 65.56 ±18.49 | 49.45 ±4.97 | 57.17 ±5.69 |
| BI | 42.83 ±5.25 | 41.15 ±3.48 | 39.13 ±1.55 | 38.08 ±2.67 | 34.71 ±5.38 | 45.67 ±1.22 | 49.04 ±2.27 | 54.15 ±23.29 | 30.09 ±1.53 | 45.78 ±7.54 | 43.02 ±5.50 | 47.73 ±2.81 |
| Simp | 0.82 ±0.02 | 0.61 ±0.12 | 0.69 ±0.12 | 0.79 ±0.05 | 0.80 ±0.03 | 0.77 ±0.01 | 0.70 ±0.05 | 0.67 ±0.12 | 0.85 ±0.02 | 0.83 ±0.02 | 0.81 ±0.02 | 0.78 ±0.02 |
| Shannon | 0.24 ±0.01 | 0.22 ±0.02 | 0.21 ±0.02 | 0.23 ±0.01 | 0.23 ±0.01 | 0.26 ±0.00 | 0.27b ±0.01 | 0.26ab ±0.01 | 0.22a ±0.01 | 0.23ab ±0.01 | 0.24ab ±0.01 | 0.25ab ±0.00 |
| N | 317.67ab ±153.82 | 188.67a ±45.61 | 1130.02ab ±149.02 | 639.27ab ±180.79 | 890.67ab ±156.76 | 1070.24b ±202.00 | 280.35ab ±110.37 | 344.73ab ±179.56 | 371.40ab ±52.34 | 134.59a ±32.85 | 263.06ab ±43.65 | 473.50b ±44.86 |
| S | 10.67 ±2.03 | 9.67 ±2.33 | 13.33 ±1.33 | 15.67 ±0.33 | 14.50 ±0.56 | 12.83 ±1.68 | 10.33 ±2.40 | 10.00 ±4.04 | 14.00 ±1.00 | 12.00 ±1.15 | 12.33 ±1.36 | 12.67 ±0.42 |

a,b Different letters mean significant differences among habitats ($P<0.05$). Comparisons were done within 0–15 and 15–30 cm depth independently

**Table 3** Average (±SE) relative and absolute (A) abundance of trophic groups, soil food web indices, and nematode community descriptors in 2006

| | 0–15 cm | | | | | | | | 15–30 cm | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ditch | Fallow | Pond | Legume | Mustard | Hedge | Riparian | Oats | Ditch | Fallow | Pond | Legume | Mustard | Hedge | Riparian | Oats |
| Ba | 0.27ab ±0.08 | 0.34ab ±0.09 | 0.25ab ±0.01 | 0.17a ±0.03 | 0.31ab ±0.03 | 0.43b ±0.04 | 0.51b ±0.03 | 0.38ab ±0.03 | 0.38ab ±0.04 | 0.53b ±0.07 | 0.20a ±0.07 | 0.33ab ±0.03 | 0.44ab ±0.08 | 0.27ab ±0.03 | 0.45ab ±0.07 | 0.30ab ±0.04 |
| Fu | 0.63ab ±0.10 | 0.46ab ±0.06 | 0.43ab ±0.16 | 0.74b ±0.03 | 0.48ab ±0.08 | 0.31a ±0.05 | 0.30a ±0.04 | 0.39ab ±0.03 | 0.43 ±0.09 | 0.27 ±0.04 | 0.45 ±0.05 | 0.49 ±0.04 | 0.30 ±0.03 | 0.26 ±0.07 | 0.21 ±0.06 | 0.33 |
| Pp | 0.08 ±0.01 | 0.19 ±0.04 | 0.32 ±0.14 | 0.08 ±0.03 | 0.20 ±0.06 | 0.24 ±0.02 | 0.18 ±0.02 | 0.22 ±0.06 | 0.18 ±0.06 | 0.20 ±0.03 | 0.33 ±0.09 | 0.17 ±0.01 | 0.25 ±0.06 | 0.38 ±0.14 | 0.32 ±0.13 | 0.35 ±0.06 |
| P | 0.00 ±0.00 | 0.01 ±0.00 | 0.00 ±0.00 | 0.01 ±0.00 | 0.00 ±0.00 | 0.01 ±0.01 | 0.01 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.01 ±0.01 | 0.00 ±0.00 | 0.02 ±0.01 | 0.01 ±0.01 | 0.01 ±0.00 |
| O | 0.02 ±0.02 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.01 ±0.01 | 0.00 ±0.00 | 0.01 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 | 0.00 ±0.00 |
| Ba A | 75.18ab ±29.03 | 57.09ab ±12.24 | 27.96a ±6.84 | 53.68ab ±10.11 | 125.20ab ±42.02 | 91.29ab ±25.96 | 53.38ab ±2.82 | 154.94b ±8.71 | 78.71ab ±43.32 | 233.34b ±70.80 | 9.01a ±3.26 | 106.54ab ±19.94 | 148.12ab ±59.18 | 45.61ab ±19.11 | 73.41ab ±18.75 | 87.77ab ±19.29 |
| Fu A | 243.72 ±105.28 | 100.40 ±39.18 | 50.39 ±23.97 | 242.45 ±41.65 | 192.80 ±72.13 | 60.26 ±9.23 | 31.92 ±6.53 | 160.61 ±9.93 | 75.06 ±45.54 | 136.06 ±51.30 | 20.39 ±1.63 | 161.63 ±43.86 | 87.30 ±29.33 | 41.47 ±17.82 | 29.96 ±2.15 | 101.51 ±33.12 |
| Pp A | 27.32 ±11.14 | 40.97 ±16.40 | 36.05 ±22.61 | 29.83 ±14.97 | 71.83 ±29.26 | 52.15 ±16.84 | 18.59 ±1.56 | 99.41 ±39.57 | 0.91 ±22.17 | 104.37 ±40.95 | 16.92 ±6.60 | 54.61 ±10.17 | 80.32 ±44.20 | 50.96 ±12.89 | 80.74 ±58.79 | 95.89 ±12.97 |
| P A | 0.13 ±0.13 | 1.36 ±0.69 | 0.00 ±0.00 | 2.29 ±0.37 | 0.63 ±0.63 | 2.34 ±2.03 | 1.04 ±0.32 | 0.58 ±0.58 | 0.26 ±0.26 | 0.89 ±0.89 | 0.17 ±0.17 | 3.22 ±3.22 | 0.14 ±0.14 | 3.46 ±1.80 | 0.74 ±0.74 | 3.31 ±1.32 |
| O A | 1.73 ±1.73 | 0.31 ±0.31 | 0.13 ±0.13 | 1.34 ±1.00 | 1.01 ±0.62 | 0.63 ±0.37 | 0.13 ±0.13 | 1.00 ±0.52 | 0.53 ±0.26 | 0.00 ±0.00 | 0.30 ±0.16 | 1.46 ±1.46 | 1.44 ±1.23 | 0.00 ±0.00 | 0.00 ±0.00 | 1.25 ±1.25 |
| EI | 54.53a ±2.48 | 64.79ab ±1.63 | 55.02a ±3.26 | 56.45a ±3.19 | 59.94ab ±6.70 | 70.95ab ±4.14 | 77.05b ±2.38 | 54.58a ±3.40 | 49.14 ±2.73 | 64.77 ±5.52 | 48.18 ±4.48 | 59.18 ±1.62 | 64.82 ±9.47 | 64.05 ±2.87 | 71.43 ±3.56 | 52.13 ±4.98 |
| SI | 9.70 ±9.70 | 4.02 ±2.03 | 1.55 ±1.55 | 6.92 ±1.61 | 22.57 ±18.76 | 37.02 ±9.80 | 15.25 ±7.00 | 3.86 ±0.98 | 6.38 ±3.82 | 5.49 ±1.20 | 6.45 ±3.64 | 10.56 ±5.37 | 5.57 ±3.01 | 32.27 ±8.38 | 34.10 ±14.10 | 20.96 ±7.31 |
| CI | 65.59b ±12.70 | 40.66ab ±6.80 | 55.98ab ±8.89 | 70.25b ±8.07 | 48.52ab ±11.69 | 23.58a ±7.18 | 18.89a ±3.12 | 49.80ab ±5.64 | 60.30ab ±10.90 | 24.44a ±3.19 | 82.61b ±13.59 | 48.33ab ±3.02 | 34.93a ±15.64 | 33.84a ±3.61 | 21.10a ±2.70 | 56.74ab ±10.71 |
| BI | 43.37b ±4.10 | 34.66ab ±1.48 | 44.56b ±2.86 | 42.24ab ±3.24 | 34.95ab ±8.29 | 25.13ab ±4.48 | 22.15a ±2.61 | 44.57b ±3.18 | 49.17b ±3.08 | 34.42ab ±5.14 | 49.63b ±3.21 | 38.99ab ±2.40 | 33.97ab ±8.49 | 30.46ab ±3.14 | 24.86a ±4.13 | 41.83ab ±3.67 |
| Simp | 0.73ab ±0.04 | 0.82b ±0.01 | 0.70ab ±0.04 | 0.59a ±0.05 | 0.83b ±0.00 | 0.82b ±0.03 | 0.82b ±0.03 | 0.83b ±0.01 | 0.79 ±0.01 | 0.81 ±0.03 | 0.56 ±0.13 | 0.79 ±0.03 | 0.80 ±0.03 | 0.80 ±0.06 | 0.78 ±0.04 | 0.83 ±0.04 |
| Shannon | 0.25 ±0.01 | 0.25 ±0.01 | 0.24 ±0.01 | 0.22 ±0.01 | 0.24 ±0.00 | 0.22 ±0.00 | 0.24 ±0.01 | 0.24 ±0.01 | 0.26b ±0.01 | 0.23ab ±0.01 | 0.20a ±0.02 | 0.24ab ±0.01 | 0.25ab ±0.01 | 0.22ab ±0.00 | 0.23ab ±0.00 | 0.22ab ±0.01 |
| N | 348.93 ±135.11 | 200.13 ±66.81 | 114.53 ±28.51 | 329.60 ±63.33 | 391.47 ±117.05 | 210.93 ±52.59 | 105.20 ±6.65 | 416.53 ±57.02 | 195.47 ±109.63 | 474.67 ±156.12 | 47.73 ±9.50 | 327.47 ±69.87 | 317.60 ±124.10 | 160.13 ±55.36 | 185.60 ±79.68 | 290.40 ±61.39 |
| S | 11.67 ±1.33 | 12.00 ±1.53 | 11.00 ±1.15 | 13.67 ±1.20 | 11.33 ±0.67 | 17.00 ±1.53 | 16.00 ±2.08 | 13.67 ±1.20 | 12.00 ±1.53 | 13.33 ±0.33 | 11.33 ±1.76 | 12.67 ±1.45 | 12.00 ±1.53 | 16.33 ±0.67 | 15.33 ±0.88 | 16.67 ±0.88 |

a, b Different letters mean significant differences among habitats ($P<0.05$). Comparisons were done within 0–15 and 15–30 cm depth independently. See Table 2 for abbreviations

**Table 4** Average (±SE) values of soil properties at 0–15 and 15–30 cm depth in 2006

| | 0–15 cm | | | | | | | | 15–30 cm | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Ditch | Fallow | Pond | Legume | Mustard | Hedge | Riparian | Oats | Ditch | Fallow | Pond | Legume | Mustard | Hedge. | Riparian | Oats |
| NO$_3^-$ (µg/g) | 0.2a ±0.1 | 0.1a ±0.0 | 0.5a ±0.1 | 0.3a ±0.0 | 0.3a ±0.1 | 0.6a ±0.1 | 2.8b ±0.8 | 0.2a ±0.0 | 0.2a ±0.1 | 0.2a ±0.1 | 0.4ab ±0.1 | 0.2a ±0.1 | 0.2a ±0.1 | 0.3a ±0.1 | 1.1b ±0.4 | 0.2a ±0.1 |
| NH$_4^+$ (µg/g) | 2.0a ±0.9 | 1.3a ±0.7 | 2.1a ±0.3 | 2.6a ±0.1 | 2.6a ±0.6 | 3.2a ±0.6 | 7.1b ±0.3 | 1.5a ±0.4 | 0.7a ±0.3 | 1.1ab ±0.5 | 1.4a ±0.3 | 2.3ab ±0.4 | 2.2ab ±0.5 | 1.5ab ±0.2 | 3.5b ±0.6 | 1.5ab ±0.7 |
| NO$_3^-$ (kg/m$^2$) | 0.0a ±0.0 | 0.0a ±0.0 | 0.1a ±0.0 | 0.0a ±0.0 | 0.1a ±0.0 | 0.1a ±0.0 | 0.4b ±0.1 | 0.0a ±0.0 | 0.0 ±0.0 | 0.0 ±0.0 | 0.1 ±0.0 | 0.0 ±0.0 | 0.0 ±0.0 | 0.1 ±0.0 | 0.2 ±0.0 | 0.0 ±0.0 |
| NH$_4^+$ (kg/m$^2$) | 0.4a ±0.2 | 0.2a ±0.1 | 0.4a ±0.1 | 0.5a ±0.0 | 0.5a ±0.1 | 0.6a ±0.1 | 1.0b ±0.0 | 0.3a ±0.1 | 0.2 ±0.1 | 0.2 ±0.1 | 0.2 ±0.1 | 0.5 ±0.1 | 0.4 ±0.1 | 0.3 ±0.0 | 0.6 ±0.1 | 0.3 ±0.2 |
| PMN (µg/g) | 4.9a ±1.5 | 6.8a ±2.7 | 12.3a ±9.4 | 7.8a ±3.2 | 9.3a ±0.8 | 14.6a ±4.4 | 83.4b ±36.2 | 7.8a ±2.5 | 9.1 ±3.4 | 9.6 ±4.1 | 2.8 ±0.9 | 10.6 ±4.8 | 24.5 ±7.6 | 4.9 ±1.1 | 24.3 ±6.7 | 4.9 ±2.0 |
| pH | 7.2 ±0.1 | 7.2 ±0.2 | 7.1 ±0.3 | 7.0 ±0.1 | 7.1 ±0.1 | 7.1 ±0.1 | 7.4 ±0.3 | 7.2 ±0.1 | 7.1 ±0.2 | 7.1 ±0.0 | 7.1 ±0.0 | 7.0 ±0.1 | 6.9 ±0.0 | 6.9 ±0.1 | 7.2 ±0.3 | 7.1 ±0.1 |
| N (kg/m$^2$) | 21.2 ±1.2 | 16.8 ±3.3 | 21.9 ±4.4 | 19.7 ±0.8 | 22.9 ±0.5 | 24.9 ±4.6 | 23.0 ±4.0 | 22.4 ±3.5 | 27.7 ±1.7 | 19.2 ±3.1 | 21.0 ±2.6 | 21.6 ±1.6 | 22.9 ±1.1 | 21.5 ±5.0 | 27.8 ±5.7 | 22.7 ±3.1 |
| C (kg/m$^2$) | 179.4ab ±19.2 | 141.1a ±24.3 | 201.0ab ±37.5 | 176.5ab ±13.1 | 228.3ab ±25.4 | 249.8ab ±44.2 | 294.4b ±38.2 | 195.4ab ±34.8 | 169.7 ±11.5 | 154.0 ±32.9 | 182.9 ±14.3 | 160.6 ±21.9 | 197.0 ±12.1 | 166.2 ±42.2 | 263.7 ±56.2 | 189.8 ±29.0 |
| N (%) | 0.1 ±0.0 | 0.1 ±0.0 | 0.1 ±0.0 | 0.1 ±0.0 | 0.1 ±0.0 | 0.1 ±0.0 | 0.2 ±0.0 | 0.1 ±0.0 | 0.1ab ±0.0 | 0.1ab ±0.0 | 0.1ab ±0.01 | 0.1ab ±0.0 | 0.1ab ±0.0 | 0.1a ±0.0 | 0.2b ±0.0 | 0.1ab ±0.0 |
| C (%) | 0.9a ±0.1 | 0.8a ±0.9 | 1.2ab ±0.0 | 0.9a ±0.1 | 1.2a ±0.1 | 1.3ab ±0.2 | 2.0b ±0.3 | 1.1a ±0.2 | 0.8a ±0.0 | 0.8a ±0.2 | 1.1ab ±0.1 | 0.8a ±0.1 | 1.0ab ±0.1 | 0.8a ±0.2 | 1.6b ±0.3 | 0.9a ±0.1 |
| P (ppm) | 40.0 ±9.8 | 27.7 ±7.8 | 36.7 ±0.1 | 28.3 ±2.1 | 35.1 ±0.6 | 28.1 ±6.2 | 32.6 ±6.7 | 33.8 ±3.8 | 28.6ab ±1.1 | 29.7ab ±7.6 | 35.7ab ±2.1 | 28.5ab ±1.7 | 37.5a ±2.4 | 16.0b ±2.2 | 23.3ab ±5.9 | 27.8ab ±4.8 |
| Soil mois. | 0.2 ±0.0 | 0.3 ±0.0 | 0.2 ±0.0 | 0.23 ±0.0 | 0.2 ±0.0 | 0.2 ±0.0 | 0.3 ±0.02 | 0.2 ±0.0 | 0.2ab ±0.0 | 0.3ab ±0.0 | 0.3b ±0.0 | 0.2ab ±0.0 | 0.2ab ±0.0 | 0.2a ±0.0 | 0.2ab ±0.0 | 0.2ab ±0.0 |
| EC (µS/cm) | 140.7a ±19.7 | 100.1a ±9.2 | 166.5a ±21.5 | 122.7a ±12.4 | 129.7a ±23.3 | 187.0a ±4.0 | 318.0b ±15.0 | 187.0a ±456.0 | 104.7a ±8.1 | 95.8a ±9.0 | 141.0ab ±25.2 | 106.8a ±8.9 | 120.3a ±6.2 | 94.3a ±11.4 | 188.3b ±6.1 | 119.7ab ±5.7 |
| BD (g/cm$^3$) | 1.3ab ±0.0 | 1.2ab ±0.1 | 1.1ab ±0.1 | 1.3ab ±0.0 | 1.3b ±0.0 | 1.3ab ±0.1 | 1.0a ±0.0 | 1.2ab ±0.1 | 1.5b ±0.1 | 1.2ab ±0.1 | 1.1a ±0.1 | 1.3ab ±0.1 | 1.3ab ±0.0 | 1.5b ±0.0 | 1.1a ±0.1 | 1.3ab ±0.1 |
| MBC (µg/g) | 124.6a ±29.6 | 169.4a ±68.4 | 112.8ab ±25.7 | 199.1ab ±14.7 | 207.9ab ±14.9 | 242.5ab ±19.9 | 367.1b ±89.5 | 238.2ab ±34.9 | 71.4ab ±35.7 | 52.0ab ±15.3 | 28.6a ±14.6 | 94.2ab ±3.4 | 136.4b ±10.9 | 81.1ab ±15.7 | 33.5a ±31.0 | 109.9ab ±1.2 |

a, b Different letters mean significant differences among habitats ($P<0.05$). Comparisons were done within 0–15 and 15–30 cm depth independently

**Table 5** Spearman rank-order correlation coefficients between nematode abundances, community descriptors, and soil properties

| | NO$_3^-$ (µg/g) | NH$_4^+$ (µg/g) | NO$_3^-$ (kg/Ha) | NH$_4^+$ (kg/Ha) | PMN (µg/g) | pH | N (kg/Ha) | C (kg/Ha) | N (%) | C (%) | Olson P | Soil mois. | EC (µS/cm) | BD (g/cm³) | MBC (µg/g) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Mesorhabditis* | **0.46** | 0.19 | **0.47** | **0.31** | **0.31** | 0.28 | 0.03 | 0.14 | 0.21 | 0.20 | −0.28 | 0.12 | 0.26 | −0.13 | −0.16 |
| *Panagrolaimus* | **0.30** | **0.47** | 0.27 | −0.03 | **0.45** | −0.05 | 0.08 | **0.38** | 0.24 | **0.52** | 0.27 | 0.13 | **0.54** | −0.23 | **0.39** |
| *Dauerlarva* | **0.36** | 0.00 | **0.36** | 0.17 | 0.11 | 0.00 | 0.11 | **0.30** | 0.18 | 0.26 | 0.00 | −0.07 | 0.17 | −0.07 | −0.08 |
| *Cruznema* | **−0.33** | −0.10 | **−0.31** | −0.07 | 0.06 | −0.17 | 0.04 | −0.04 | −0.06 | −0.12 | 0.16 | −0.04 | −0.28 | 0.11 | 0.15 |
| *Acrobeles* | 0.25 | 0.00 | 0.18 | 0.06 | 0.02 | −0.13 | 0.05 | 0.11 | 0.26 | 0.27 | 0.09 | 0.27 | 0.09 | **−0.32** | −0.15 |
| *Acrobeloides* | −0.23 | **−0.40** | −0.22 | 0.00 | −0.04 | 0.10 | 0.03 | −0.27 | −0.08 | **−0.33** | −0.07 | 0.02 | −0.16 | 0.08 | −0.24 |
| *Plectus* | 0.19 | 0.07 | 0.20 | **0.33** | −0.09 | −0.15 | **0.30** | 0.22 | 0.18 | 0.14 | 0.11 | −0.06 | 0.10 | 0.08 | −0.12 |
| *Cephalobidae* | −0.04 | −0.16 | 0.00 | 0.02 | 0.14 | −0.02 | 0.27 | 0.17 | 0.23 | 0.11 | 0.17 | −0.28 | −0.03 | **0.30** | 0.20 |
| *Metacrolobus* | 0.27 | 0.16 | **0.31** | 0.22 | **0.29** | 0.06 | 0.13 | 0.17 | 0.19 | 0.11 | −0.22 | 0.09 | 0.19 | −0.04 | 0.15 |
| *Wilsonema* | 0.26 | **0.36** | 0.20 | **0.36** | **0.33** | **0.39** | −0.06 | 0.21 | 0.27 | **0.34** | **−0.33** | 0.01 | **0.37** | **−0.33** | −0.15 |
| *Prismatolaimus* | 0.28 | 0.21 | **0.32** | **0.43** | 0.14 | 0.05 | 0.16 | 0.21 | 0.11 | 0.14 | −0.21 | −0.01 | 0.25 | 0.05 | −0.10 |
| *Alaimus* | 0.01 | 0.14 | −0.05 | 0.23 | 0.26 | 0.24 | −0.13 | 0.02 | 0.11 | 0.13 | **−0.32** | 0.15 | 0.22 | 0.26 | −0.02 |
| *Aphelenchus* | **−0.52** | −0.24 | **−0.47** | **−0.43** | −0.19 | −0.02 | −0.15 | **−0.39** | **−0.40** | **−0.49** | −0.09 | −0.05 | **−0.36** | 0.26 | 0.18 |
| *Tylenchidae* | 0.07 | −0.05 | 0.02 | 0.04 | 0.08 | −0.05 | 0.22 | 0.23 | **0.30** | 0.27 | **0.30** | 0.13 | 0.21 | −0.15 | −0.07 |
| *Tylencholaimus* | 0.24 | 0.06 | **0.31** | 0.06 | 0.10 | −0.05 | −0.04 | 0.05 | −0.17 | −0.03 | −0.17 | −0.11 | 0.11 | 0.25 | 0.19 |
| *Paratylenchus* | 0.21 | 0.20 | 0.20 | **0.30** | 0.09 | 0.26 | −0.24 | −0.02 | −0.07 | 0.02 | **−0.53** | −0.15 | 0.04 | −0.07 | −0.18 |
| *Psilenchus* | 0.14 | −0.02 | 0.07 | 0.01 | **−0.30** | −0.05 | 0.07 | 0.08 | 0.24 | 0.19 | 0.15 | 0.12 | 0.22 | −0.18 | −0.26 |
| *Pratylenchus* | 0.16 | −0.14 | 0.21 | 0.20 | 0.18 | −0.05 | 0.15 | 0.00 | 0.10 | −0.07 | **−0.38** | −0.08 | 0.09 | 0.09 | −0.15 |
| *Tylenchorhynchus* | **−0.32** | −0.03 | −0.28 | 0.11 | 0.08 | 0.01 | 0.17 | 0.01 | 0.04 | −0.09 | 0.27 | −0.17 | −0.18 | 0.04 | 0.13 |
| *Xiphinema* | −0.11 | −0.04 | −0.07 | 0.01 | 0.02 | 0.04 | **−0.37** | **−0.31** | **−0.37** | −0.28 | **−0.32** | −0.02 | −0.10 | −0.01 | −0.01 |
| *Discolaimus* | −0.09 | 0.01 | −0.05 | 0.14 | −0.14 | −0.10 | 0.18 | 0.10 | −0.02 | −0.09 | −0.16 | −0.28 | −0.15 | **0.33** | 0.03 |
| *Ba* | 0.20 | 0.03 | 0.21 | **0.30** | **0.41** | 0.07 | 0.13 | 0.16 | 0.22 | 0.16 | −0.04 | 0.03 | 0.12 | −0.06 | 0.03 |
| *Fu* | −0.25 | −0.15 | −0.27 | **−0.52** | −0.24 | −0.03 | −0.12 | −0.23 | −0.20 | −0.18 | 0.19 | 0.22 | −0.15 | −0.03 | 0.22 |
| *Pp* | 0.05 | 0.04 | 0.06 | **0.34** | 0.03 | 0.00 | 0.11 | 0.11 | 0.14 | 0.07 | −0.01 | −0.18 | 0.09 | −0.01 | −0.21 |
| *Ba A* | −0.16 | 0.12 | −0.10 | 0.09 | **0.33** | 0.06 | 0.20 | 0.22 | 0.06 | 0.11 | 0.05 | −0.19 | 0.04 | 0.10 | 0.23 |
| *Fu A* | **−0.30** | 0.11 | −0.24 | −0.27 | 0.11 | −0.01 | 0.07 | 0.03 | −0.15 | −0.06 | 0.13 | −0.07 | −0.06 | 0.13 | **0.41** |
| *Pp A* | −0.18 | 0.14 | −0.11 | 0.18 | 0.12 | 0.06 | 0.15 | 0.14 | −0.03 | 0.00 | 0.04 | **−0.37** | 0.00 | 0.21 | 0.04 |
| *EI* | **0.39** | **0.47** | **0.40** | **0.29** | **0.51** | −0.04 | 0.03 | **0.37** | 0.23 | **0.46** | −0.04 | 0.03 | 0.29 | −0.18 | 0.20 |
| *SI* | 0.26 | 0.27 | **0.32** | **0.38** | 0.17 | −0.01 | 0.12 | 0.20 | 0.01 | 0.10 | −0.27 | −0.09 | 0.24 | 0.13 | −0.03 |
| *CI* | **−0.37** | **−0.32** | **−0.39** | **−0.39** | **−0.46** | 0.00 | −0.05 | **−0.30** | −0.22 | **−0.34** | 0.13 | 0.06 | −0.23 | 0.09 | −0.06 |
| *BI* | **−0.39** | **−0.47** | **−0.41** | **−0.35** | **−0.48** | 0.04 | −0.03 | **−0.36** | −0.18 | **−0.43** | 0.09 | 0.00 | **−0.30** | 0.10 | −0.18 |
| *Simpon* | 0.15 | −0.05 | 0.21 | 0.18 | **0.29** | −0.13 | 0.21 | 0.18 | 0.10 | 0.11 | 0.03 | −0.06 | 0.08 | 0.07 | 0.17 |
| *S* | **0.29** | 0.19 | **0.33** | **0.32** | **0.31** | 0.03 | 0.11 | 0.16 | 0.16 | 0.14 | −0.24 | 0.05 | **0.30** | −0.03 | 0.11 |

See Table 2 for abbreviations. Bold numbers indicate significant correlation ($p<0.05$). Dependent and independent variables not showing any significant relationship have been omitted
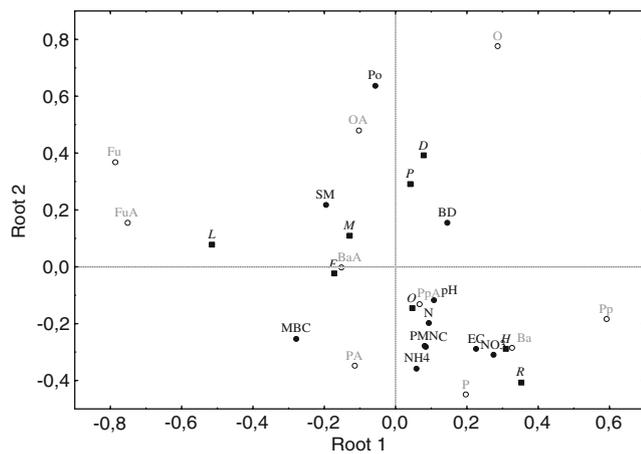
**Fig. 2** CCA biplot showing associations between nematode trophic groups (*white circles*), soil properties (*dark circles*), and farm habitats (*dark squares*). Note that continuous variables define a gradient from higher values (where the variable is plotted) to lower values situated in the opposite part of the graph trough an axis that passes through the point (0,0). Habitats: *D* Ditch, *F* Fallow, *P* Ponds, *L* Legumes, *M* Mustard; *H* Hedgerows; *R* Riparian Corridor. Soil properties: *Po* Phosphorous, *SM* Soil moisture, *BD* Bulk density, *MBC* Microbial biomass carbon, *PMN* Potential mineralizable nitrogen, *C* Total C, *N* Total N; *EC* Electrical conductivity; *NH4* $NH_4^+ - N$, *NO3* $NO_3^- - N$ (see Table 2 for nematode trophic groups abbreviations)

(Category 2), and soil food web indices (Category 3) to determine each subset of variables that best discriminated differences among the habitats. In addition, the difference among habitats was then tested by including in the model only the variables that provided significant discrimination (Tables 6, 7, and 8; soil properties, absolute abundances of nematodes, and soil food web indices).

### Category 1: Habitat discrimination by soil properties

The model was significant for soil properties (Wilks' Lambda=0.012, $F_{(77,181)}=2.56$, $P<0.0000$). Differences among habitats (indicated by bold numbers in Table 6) show that the riparian corridor had significantly different soil properties than the other habitats, and ponds had

different properties than all habitats except the fallow field. Soil properties in ditches were also different from the riparian area and from the mustard field (Table 6).

These differences are represented as a cluster tree in Fig. 3a., used to facilitate visualization of the differences detected between habitats. In the cluster resulting from the analyses of soil properties, the only habitat not associated with agricultural disturbance (the riparian corridor) formed a separate cluster. The model separated habitats into two groups: the riparian corridor in a single cluster and all the others in another group, in which ponds were the most different habitat from the others.

### Category 2: Habitat discrimination by nematode taxa abundances

Discriminant analysis was also performed with the absolute abundances of nematodes. Of the 35 nematode taxa included in the analysis, 21 were retained in the final model, which had a high resolution capacity (Wilks' Lambda=0.00021, $F_{(147,144)}=2.52$, $P<0.0000$). The greatest differences in terms of nematode community composition among groups were found between legumes and hedgerows and between legumes and oats (Table 7), indicating greater differences between winter cover crop management practices than between uncultivated and cultivated habitats. The resulting cluster tree (Fig. 3b.) shows hedgerows in a single cluster and all the other habitats in another one.

### Category 3: Habitat discrimination by soil food web indices

For the discriminant analysis performed on the soil food web indices, the model included all of the indices and was highly significant (Wilks' Lambda=0.18, $F_{(28,134)}=2.94$, $P<0.0000$). SI contributed most to the model discrimination, followed by EI, CI, and BI. Greatest differences were

**Table 6** Squared Mahalanobis distances between group centroids in the discrimination between the eight habitats by soil properties

|          | P    | D      | R      | L      | F      | M      | HR     | O      |
|----------|------|--------|--------|--------|--------|--------|--------|--------|
| Ponds    | 0.00 | **15.45\*** | **37.57\*** | **17.52\*** | 14.41  | **22.64\*** | **22.96\*** | **15.84\*** |
| Ditches  |      | 0.00   | **67.82\*** | 7.47   | 8.43   | **15.78\*** | 11.84  | 6.07   |
| Riparian |      |        | 0.00   | **62.21\*** | **68.65\*** | **70.20\*** | **56.53\*** | **64.20\*** |
| Legume   |      |        |        | 0.00   | 5.46   | 6.65   | 3.69   | 6.76   |
| Fallow   |      |        |        |        | 0.00   | 5.82   | 9.37   | 4.37   |
| Mustard  |      |        |        |        |        | 0.00   | 9.31   | 8.98   |
| Hedgerow |      |        |        |        |        |        | 0.00   | 6.69   |
| Oats     |      |        |        |        |        |        |        | 0.00   |

Bold numbers marked with * indicate significant differences among groups for soil properties ($P<0.05$). Higher numerical values indicate greater distances (differences) among groups

*P* Ponds, *D* ditches, *R* riparian corridor, *L* legumes, *F* fallow, *M* mustard, *HR* hedgerows, *O* oats

**Table 7** Squared Mahalanobis distances between group centroids in the discrimination between the eight habitats by nematode taxa abundances

|  | P | D | R | L | F | M | HR | O |
|---|---|---|---|---|---|---|---|---|
| Ponds | 0.0 | 25.6 | 16.4 | **79.8*** | 19.8 | 11.8 | **56.9*** | **46.7*** |
| Ditches |  | 0.0 | **45.4*** | 35.7 | 26.7 | 34.2 | **65.0*** | **43.0*** |
| Riparian |  |  | 0.0 | **109.4*** | 30.8 | 25.0 | **58.2*** | **67.5*** |
| Legume |  |  |  | 0.0 | 75.9 | **103.9*** | **135.1*** | **124.8*** |
| Fallow |  |  |  |  | 0.0 | 21.2 | **76.3*** | **48.2*** |
| Mustard |  |  |  |  |  | 0.0 | **76.9*** | 35.2 |
| Hedgerow |  |  |  |  |  |  | 0.0 | **88.5*** |
| Oats |  |  |  |  |  |  |  | 0.0 |

Bold numbers marked with * indicate significant differences among groups for soil properties ($P<0.05$). Higher numerical values indicate greater distances (differences) among groups.

*P* Ponds, *D* ditches, *R* riparian corridor, *L* legumes, *F* fallow, *M* mustard, *HR* hedgerows, *O* oats

found between the riparian corridor and hedgerows vs ponds and ditches (Table 8).

The cluster analysis provided a tree in which hedgerows and riparian corridor are grouped in a cluster separated from the other habitats (Fig. 3c.). Two of the winter treatments on the north field, mustard and fallow, group together, separated from ponds and ditches, which are closely related and with the north field legumes and oat treatments sequentially included. Therefore, soil food web indices discriminated highly between the two habitats subjected to least disturbance (the riparian corridor and hedgerows) and the two habitats most disturbed (ponds and ditches). Surprisingly, the legume field was not included in the same cluster as fallow and mustard (the three habitats were in the north field), being significantly different from fallow (but not from mustard).

To validate the model and the cluster tree resulting from the analyses of the soil food web indices, that is, to ensure that those differences in the soil food web among habitats were not already present before applying the cover crops, 2006 data were re-analyzed using the 2005 classification of five habitats, using discriminant analysis. The resulting model was not significant (Wilks' Lambda=0.61, $F_{(14,76)}=$ 1.52, $P<0.1259$), and the EI and SI were excluded from the model. The 2005 cluster that resulted from this analysis did not show the same pattern found for the 2006 classification, indicating that the difference between the mustard, oat, legume, and fallow fields in 2006 are indeed related to effects of the cover crop treatments and that detected differences were not already present the previous year when the field was homogeneously managed.

## Discussion

Biological assemblages are structured by the myriad historical, physical, and chemical variables that define ecosystem properties. The assemblages can be dramatically changed by chemical and physical soil perturbations, especially in agroecosystems. For example, changes in soil management lead to different soil communities (Sánchez-Moreno et al. 2006), and changes in community composition lead to different rates of organism functions and ecosystem services (Cragg and Bardgett 2001). Soil organisms that exhibit characteristics of diversity and abundance often can be used as bioindicators (Breure

**Table 8** Squared Mahalanobis distances between group centroids in the discrimination between the eight habitats by soil food web indices

|  | P | D | R | L | F | M | HR | O |
|---|---|---|---|---|---|---|---|---|
| Ponds | 0.0 | 0.6 | **15.7*** | 1.0 | **6.7*** | **5.6*** | **14.2*** | 3.1 |
| Ditches |  | 0.0 | **13.3*** | 1.4 | **5.3*** | 4.5 | **10.8*** | 1.6 |
| Riparian |  |  | 0.0 | **9.4*** | **5.7*** | **6.3*** | 1.9 | **12.1*** |
| Legume |  |  |  | 0.0 | **4.0*** | 2.9 | **9.3*** | 3.2 |
| Fallow |  |  |  |  | 0.0 | 1.2 | **7.3*** | 3.4 |
| Mustard |  |  |  |  |  | 0.0 | **6.4*** | 2.2 |
| Hedgerow |  |  |  |  |  |  | 0.0 | **9.2*** |
| Oats |  |  |  |  |  |  |  | 0.0 |

Bold numbers marked with * indicate significant differences among groups for soil properties ($P<0.05$). Higher numerical values indicate greater distances (differences) among groups

*P* Ponds, *D* ditches, *R* riparian corridor, *L* legumes, *F* fallow, *M* mustard, *HR* hedgerows, *O* oats

**Fig. 3** Cluster diagrams resulting from the distance matrix of eight habitats (2006) as a function of soil properties ($NO_3^- - N$, $NH_4^+ - N$, PMN, pH, N, C, P, SM, EC, BD, and MBC; see Table 5 for abbreviations) (**a**); of the absolute abundance of nematode taxa (**b**) (all taxa included, see Table 1), and of the soil food indices values (EI, SI, CI, and BI) (**c**)
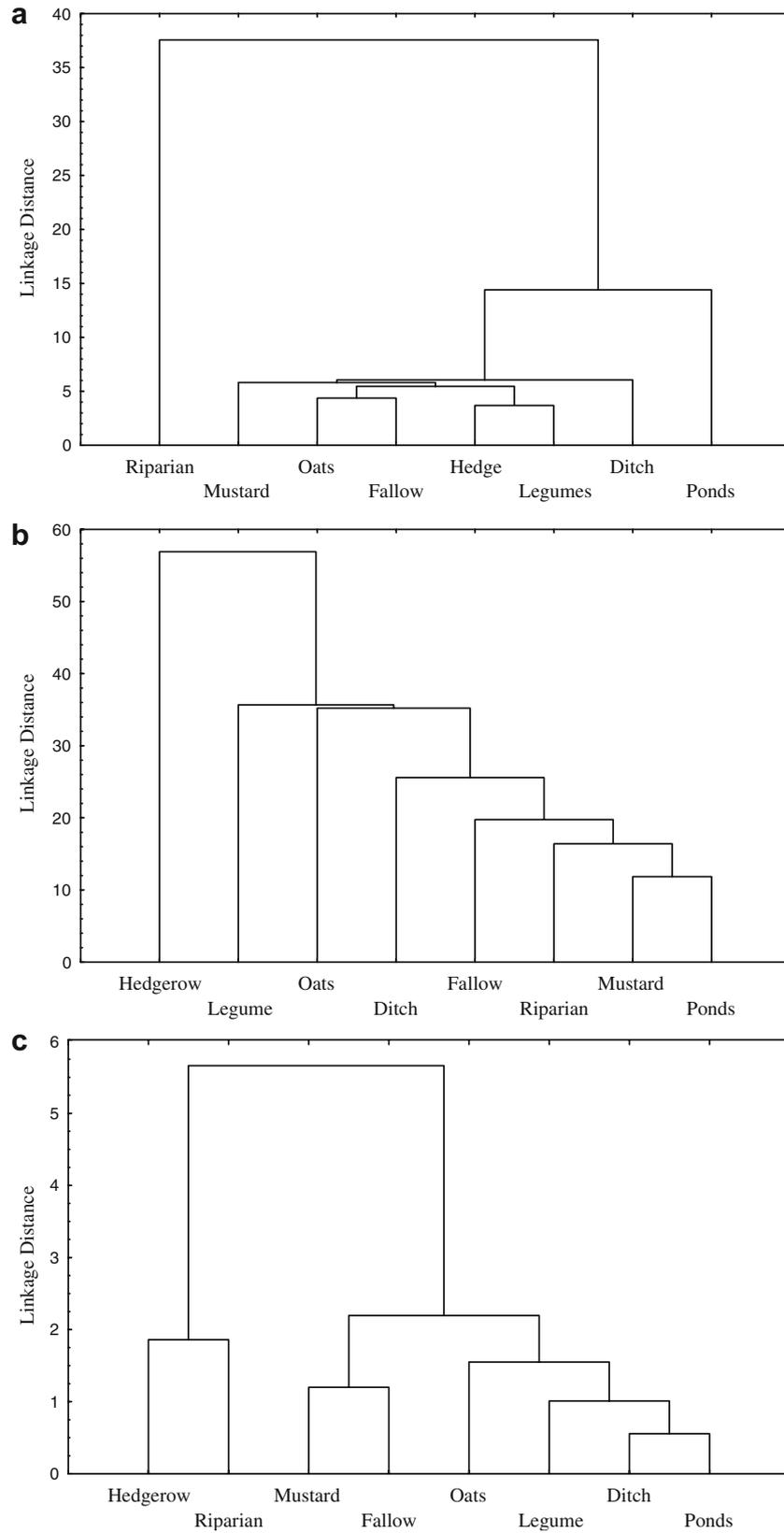
et al. 2005). Within soil animals, nematodes have been broadly used as ecosystem health indicators at very different scales (Ekschmitt et al. 2001, 2003; Neher 2001; Mulder et al. 2005). Nematode faunae are usually richer in non-cultivated lands, and nematode diversity increases within a soil type when arable fields are abandoned (Háněl 2003).

The nematode fauna, like every other biological soil assemblage, is physically distributed in continuous gradients and in discontinuous aggregations across the landscape, so differences in nematode abundance among habitats may be too small, or affected taxa too scarce, to be detected when landscape patterns are analyzed as discrete land units. The gradients and discontinuities of organism distribution may be responsible for the sometimes unclear differences in trophic group sizes and soil food web indices among habitats in this and other studies. Higher nematode trophic levels, such as predators and omnivores, are generally less abundant in arable fields than in natural areas due to their greater sensitivity to nitrogen fertilizers, tillage, cropping, and pesticides (Fiscus and Neher 2002; Tenuta and Ferris 2004). In this study, as expected, predators tended to be more abundant in the undisturbed riparian corridor than in the arable fields. However, there were some unexpected associations between nematode trophic groups and field usage. Bacterial-feeding nematodes were expected to be more abundant in the legume field due to lower C/N ratios of the organic inputs (Wardle et al. 2003), but actually lower absolute and relative abundance of bacterial-feeders were detected in the legume fields at both 0–15 and 15–30 cm depth, while fungal-feeding nematodes were more abundant than bacterial-feeders. Thus, the CI, indicator of fungal-mediated decomposition pathways, was higher in legumes at 0–15 cm depth in 2006. Some leguminous species are known to support high populations of fungi in the rhizosphere. For example, in comparison to 14 other plant species, *Lupinus luteus* was most effective in supporting fungal biomass in rhizosphere soil (Appuhn and Joergensen 2006). Also unexpectedly, high values of the EI, an indicator of rapid organic matter decomposition mediated by bacteria, were associated with hedgerows and the riparian corridor, clearly responding to high C and N soil content in those areas. Indeed, organic matter content was surprisingly high in the riparian area, perhaps reflecting years of runoff from the agricultural areas and high organic matter inputs with little disturbance. The enriched conditions led to a nematode fauna with high values of both the SI and the EI. Nematode movement across habitats, probably associated with run-off water, may explain the presence of some nematode taxa in certain habitats, for example, the presence, even if at very low abundance, of *Meloidogyne* juveniles in the ponds that collect run-off water from the fields.

Abundances of bacterial feeders were in general associated with higher measurements of soil $NO_3^- - N$ and $NH_4^+ - N$, as found in many studies (Brussaard et al. 1995; Forge and Simard 2001; Savin et al. 2001; Postma-Blaauw et al. 2005). Only one nematode taxon, *Cruznema*, was negatively correlated with soil $NO_3^- - N$ and $NH_4^+ - N$. *Cruznema* is a very effective grazer of bacteria (under conditions favorable for its activity), producing a significant positive effect on bacterial biomass and the content of inorganic N in soil (Ferris et al. 1997; Fu et al. 2005), so a positive relationship between its abundance and soil N was expected. *Aphelenchus*, the most abundant fungal-feeder in the farmscale, was negatively correlated with $NO_3^- - N$, $NH_4^+ - N$, and total soil C. The contribution of fungal-feeding nematodes to N mineralization is smaller than that of bacterial-feeding nematodes (Okada and Ferris 2001), and a negative relationship between the CI, indicator of fungal-mediated organic matter decomposition pathways, and the amount of $NO_3^- - N$, $NH_4^+ - N$ in the soil was not unexpected (Ferris and Matute 2003). Previous studies have shown positive relationships between the CI and soil C (Stirling and Lodge 2005), but we found negative correlation coefficients between CI and soil C content, and higher CI values in the legume field (0–15 cm, 2006), probably resulting from short-term rhizosphere interactions due to fungi and the associated increase in MBC (Appuhn and Joergensen 2006). The BI was related to soil properties similarly to the CI, indicating a more basal and stressed conditions of the soil food web in ponds and ditches.

Consistent with previous studies, the EI was a good indicator of the amount of N in the soil (Ferris et al. 2004; Wang et al. 2006), correlated with the contents of total C and N, $NH_4^+ - N$, and $NO_3^- - N$ of soil. The SI, indicator of soil food web connectance and length, is often negatively correlated with total soil N content, at least in disturbed systems (Berkelmans et al. 2003; Sánchez-Moreno et al. 2006). Besides higher values of the EI, the SI was also higher in the riparian corridor. Our results therefore suggest that predators and complex soil food webs may coexist with enrichment-opportunistic nematodes and that organisms in the higher levels of the soil food web can survive in enriched soils when physical perturbation is absent. In fact, such systems, with abundant microbivorous nematodes, would be supplying resources to higher trophic levels (Ferris and Bongers 2006). Significant correlation coefficients were also found between diversity indices and N mineralization as inferred from net changes in $NH_4^+ - N$, $NO_3^- - N$ and total N of soil. However, no causal relationships can be inferred, and such relationships may be mainly casual, determined by autocorrelated spatial patterns produced by the occupancy of the riparian corridor by both predator and bacterial-feeding nematodes.

There were few significant differences in the abundance of nematode taxa or in taxa richness among habitats. Nonetheless, soil food web condition and ecosystem functioning differed among habitats, indicating that the functional consequences of the relationships between dynamic assemblages of organisms are not fully reflected by the taxonomic composition of biological communities.

When there is taxonomic diversity at a trophic level or in a functional guild, elimination of one or more taxa may not affect soil food web function. However, in functional guilds or trophic levels with less taxonomic diversity, reduction in abundance of one taxon may have a significant effect on functional characteristics of the soil food web. In disturbed systems, there is often lower diversity in the higher trophic levels so that small taxonomic changes may result in large effects on the SI and on the regulatory function of predation on opportunistic species. Indeed, the most sensitive nematode taxa rapidly disappear with soil disturbance and many years may be necessary for recovery of taxonomic richness and the functions with which those organisms are associated (Sánchez-Moreno et al. 2006).

Scale is a central theme in ecology because changes in the resolution of observation allow the detection of occult patterns not detectable at other scales (Levin 1992). Similarly, observing the system at different functional resolution (from soil properties to nematode taxa abundance and soil food web indices) may be a critical factor in determining belowground patterns at the landscape level. While soil properties mainly discriminated two groups of habitats (riparian corridor vs all the other habitats that were or had been tilled in the past), the use of taxonomic diversity and soil food web indices revealed other patterns. Abundances of nematode taxa as predictor variables introduce biological traits into the model, including the capacity of different species to persist in each habitat. Nematode faunae often show high resolution capacity in the discrimination of different habitats; Hánĕl (1995) found very different nematode assemblages in fields, fallow, meadows, and forests, and Popovici and Ciobanu (2000) found significant relationships between nematode faunal composition and habitat characteristics, including vegetation. Using other soil organisms, Kapusta et al. (2003) found that soil properties discriminated between different habitats much more distinctly than composition of the enchytraeid community. In this study, however, nematode abundances discriminated habitats in a very different way than the measured soil properties or soil food web indices. Abundance of nematode taxa primarily separated oats and hedgerows from the other habitats and did not discriminate between cultivated and non-cultivated areas, suggesting that both short-term (rotation) and longer-term (woody perennial) factors play a role in abundance. Additionally, nematode taxa

did not reflect the specific soil properties detected in the riparian corridor.

At a farm level, soil food web indices provided a more structured ordination than nematode abundances; they linked pond and ditches, mustard and fallow fields, and hedgerows and riparian corridors into single clusters. Of all the soil food web indices, the SI was the best indicator of farmscape diversity patterns. While functional groups are "abstractions that help us to view more clearly the resulting emerging properties and processes that have became part of that environment" (Brussaard 1998), soil food web indices also reflect relationships between functional guilds, for example, weighting the relative contribution of fungal- and bacterial-feeding organisms to organic matter decomposition. Indeed, habitat discrimination by soil food web indices seems to be more strongly related than nematode community composition to soil functioning (as inferred by soil properties), indicating that ecosystem functions are probably driven by complex assemblages rather than by individual taxa. In the present study, soil food web indices based on the nematode fauna provided a better indicator of both farmscape patterns and soil functions than that indicated by nematode taxa abundance. Thus, more complex soil food web attributes reflect soil functions that were partially described by using soil properties as indicators.

## Conclusions

The effects of different farm management practices on the function of soil food webs are not directly predictable from nematode faunal composition. At some trophic levels, small differences in nematode community composition had substantial effects on nematode functional guild structure and, therefore, large effects on the function of the soil food web. Aboveground farmscale patterns, however, were reflected in soil food web indices, especially the SI. In less disturbed areas, enrichment and structure attributes may coexist in the soil food web, providing services of enhanced soil fertility and regulation of opportunistic species.

## References

Appuhn A, Joergensen RG (2006) Microbial colonisation of roots as a function of plant species. Soil Biol Biochem. 38:1040–1051

Barker KR (1985) Nematode extraction and bioassays. In: Barker KR, Carter CC, Sasser JN (eds) An advanced treatise on meloidogyne. Vol. 2. Methodology. North Carolina State University Graphics, Raleigh, NC, USA, pp 19–35

Bengtsson J, Ahnstrom J, Weibull AC (2005) The effects of organic agriculture on biodiversity and abundance: a meta-analysis. J Appl Ecol 42:261–269

Berkelmans R, Ferris H, Tenuta M, van Bruggen AHC (2003) Effects of long-term crop management on nematode trophic levels other than plant feeders disappear after 1 year of disruptive soil management. Appl Soil Ecol 23:223–235

Bongers T, Bongers M (1998) Functional diversity of nematodes. Appl Soil Ecol 10:239–251

Bossio DA, Scow KM (1995) Impact of carbon and flooding on the metabolic diversity of microbial communities in soils. Appl Environ Microbiol 61:4043–4050

Breure AM, Mulder C, Römbke J, Ruf A (2005) Ecological classifications and assessment concepts in soil protection. Ecotox Environ Safety 62:211–229

Brussaard L (1998) Soil fauna, guild, functional groups and ecosystem processes. Appl Soil Ecol 9:123–135

Brussaard L, Noordhuis R, Geurs M, Bouwman LA (1995) Nitrogen mineralization in soil microcosm with or without bacteriovorous nematodes and nematophagous mites. Acta Zool Fenn 196:15–21

Brussaard L, de Ruiter PC, Brown GG (2007) Soil Biodiversity for agriculture sustainability. Agric Ecosyst Environ 121:233–244

Burger M, Jackson LE (2003) Microbial immobilization of ammonium and nitrate in relation to ammonification and nitrification rates in organic and conventional cropping systems. Soil Biol Biochem 35:29–36

Cragg RG, Bardgett RD (2001) How changes in soil faunal diversity and composition within a trophic group influence decomposition processes. Soil Biol Biochem 33:2073–2081

Didden WAM, Marinissen JCY, Vreekenbuijs MJ, Burgers SLGE, Defluiter R, Geurs M, Brusaard L (1994) Soil mesofauna and macrofauna in 2 agricultural systems - Factors affecting population dynamics and evaluation of their role in carbon and nitrogen dynamics. Agric Ecosyst Environ 51:171–186

Ekschmitt K, Bakonyi G, Bongers M, Bongers T, Boström S, Dogan H, Harrison A, Nagy P, O'Donnell AG, Papatheodorou EM, Sohlenius B, Stamou GP, Wolters V (2001) Nematode community structure as indicator of soil functioning in European grassland. Eur J Soil Biol 37:263–268

Ekschmitt E, Stierhof T, Dauber J, Kreimes K, Wolters V (2003) On the quality of soil biodiversity indicators: abiotic parameters as predictor of soil faunal richness at different spatial scales. Agric Ecosyst Environ 98:273–283

ESRI (2005) Arcview. ESRI, Redlands, CA, USA

Ferris H, Bongers T (2006) Nematode indicators of organic enrichment. J Nematol 38:3–12

Ferris H, Matute MM (2003) Structural and functional succession in the nematode fauna of a soil food web. Appl Soil Ecol 23:93–110

Ferris H, Venette RC, Lau SS (1997) Population energetics of bacterial-feeding nematodes: Carbon and nitrogen budgets. Soil Biol Biochem 29:1183–1194

Ferris H, Bongers T, de Goede RGM (2001) A framework for soil food web diagnostics: extension of the nematode faunal analysis concept. Appl Soil Ecol 18:13–29

Ferris H, Venette RC, Scow KM (2004) Soil management to enhance bacteriovore and fungivore nematode populations and their nitrogen mineralisation function. Appl Soil Ecol 25:19–35

Fiscus DA, Neher DA (2002) Distinguishing sensitivity of free-leaving soil nematode genera to physical and chemical disturbances. Ecol Appl 12:565–575

Fitter AH, Gilligan CA, Hollingworth K, Kleczkowski A, Twyman RM, Pitchford JW, the members of the Nerc Soil Biodiversity Program (2005) Biodiversity and ecosystem function in soil. Funct Ecol 19:369–377

Forge TA, Simard SW (2001) Structure of nematode communities in forest soils of southern British Columbia: relationships to nitrogen mineralization and effects of clearcut harvesting and fertilization. Biol Fert Soils 34:170–178

Fu S, Ferris H, Brown D, Plant R (2005) Does positive feedback effect of nematodes on the biomass and activity of their bacteria prey vary with nematode species and population size? Soil Biol Biochem 37:1979–1987

Fuller RM, Devereux BJ, Gillings S, Amable GS, Hill RA (2005) Indices of bird-habitat preference from field surveys of birds and remote sensing of land cover: a study of south-eastern England with wider implications for conservation and biodiversity assessment. Global Ecol Biogeogr 14:223–239

Háněl L (1995) Secondary succesional stages of soil nematodes in cambisols of south Bohemia. Nematologica 41:197–218

Háněl L (2003) Recovery of soil nematode populations from cropping stress by natural secondary succession to meadow land. Appl Soil Ecol 22:255–270

Hunt HW, Wall DH (2002) Modelling the effects of loss of biodiversity on ecosystem function. Global Change Biol 8:33–50

Kapusta P, Sobczyk L, Rozen A, Weiner J (2003) Species diversity and spacial distribution of enchytraeid communities in forest soil: effects of habitat characteristics and heavy metal contamination. Appl Soil Ecol 23:187–198

Levin SA (1992) The problem of pattern and scale in ecology. Ecology 73:1943–1967

Liang WJ, Li Q, Jiang Y, Neher DA (2005) Nematode faunal analysis in an aquic brown soil fertilised with slow-release urea, Northeast China. Appl Soil Ecol 29:185–192

Mäder P, Fliessbach A, Dubois D, Gunst L, Fried P, Niggli U (2002) Soil fertility and biodiversity in organic farming. Science 296:1694–1697

Miranda KM, Espey MG, Wink DA (2001) A rapid, simple spectrophotometric method for simultaneous detection of nitrate and nitrite. Nitric Oxide Biol Chem 5:62–71

Mulder C, Schouten AJ, Hund-Rinke K, Breure AM (2005) The use of nematodes in ecological soil classification and assessment concepts. Ecotoxicol Environ Safety 62:278–289

Neher D (2001) Role of nematodes in soil health and their use as indicators. J Nematol 33:161–168

Okada H, Ferris H (2001) Effect of temperature on growth and nitrogen mineralization of fungi and fungal-feeding nematodes. Plant Soil 234:253–262

Olsen SR, Sommers LE (1982) Phosphorus. In: Page AL (ed) Methods of soil analysis: Part 2. Chemical and microbiological properties. ASA Monograph Number 9, Madison, WI, pp 403–430

Pella E (1990) Combustion gas analyzer method for total carbon and total nitrogen. In: Pella E (ed) Elemental organic analysis 1. Historical Developments. Am. Lab, pp 1–16

Popovici I, Ciobanu M (2000) Diversity and distribution of nematode community in grassland from Romania in relation to vegetation and soil characteristics. Appl Soil Ecol 14:27–36

Postma-Blaauw MB, de Vries FT, de Goede RGM, Bloem J, Faber JH, Brussaard L (2005) Within-trophic group interactions of bacter-ivorous nematode species and their effects on the bacterial community and nitrogen mineralization. Oecologia 142:428–439

Rhoades JD (1982) Soluble salts. In: Page AL (ed) Methods of soil analysis: Part 2. Chemical and microbiological properties. ASA Monograph Number 9, Madison, WI, pp 167–179

Sánchez-Moreno S, Minoshima H, Ferris H, Jackson LE (2006) Linking soil properties and nematode community composition: effects of soil management on soil food webs. Nematology 8:703–715

Savin MC, Gorres JH, Neher DA, Amador JA (2001) Uncoupling of carbon and nitrogen mineralization: role of microvorous nematodes. Soil Biol Biochem 33:1463–1472

Shannon CE (1948) A mathematical theory of communication. Bell Syst Tech J 27:379–423

Simpson EH (1949) Measurement of diversity. Nature 163:688

Smukler S, Jackson L, Murphee L, Yokota R, Koike S, Smith R (2007) Transition to large-scale organic vegetable production in the Salinas Valley. Agric Ecosyst Environ (in press)

Soil Survey Staff (2006) National soil survey handbook. US Department of Agriculture, Natural Resources Conservation Service. http://soils.usda.gov/technical/handbook/

StatSoft I (1996) Statistica for Windows (Computer Program Manual). StatSoft I, Tulsa, OK, 74104, USA

Steenwerth KL, Jackson LE, Calderon FJ, Stromberg MR, Scow KM (2003) Soil microbial community composition and land use history in cultivated and grassland ecosystems of coastal California. Soil Biol Biochem 35:489–500

Stirling GR, Lodge GM (2005) A survey of Australian temperate pastures in summer and winter rainfall zones: soil nematodes, chemical, and biochemical properties. Austr J Soil Res 43:887–904

Tenuta M, Ferris H (2004) Sensitivity of nematode life-history groups to ions and osmotic tensions of nitrogenous solutions. J Nematol 36:85–94

USDA-SCS (1972) Soil survey of Yolo County, California. Washington, DC USDA, Soil Conservation Service, in cooperation with University of California Agricultural Experiment Station, 102 pp

US Salinity Laboratory Staff (1954) pH reading of saturated soil paste. In: Richards LA (ed) Diagnosis and improvement of saline and alkali soils. USDA Agricultural Handbook 60. US Government Printing Office, Washington, DC, USA, p 102

Van Mansvelt JD, Stobbelaar DJ, Hendriks K (1998) Comparison of landscape features in organic and conventional farming systems. Lands Urban Plan 41:209–227

Vance ED, Brookes C, Jenkinson DS (1987) An extraction method for measuring soil microbial biomass carbon. Soil Biol Biochem 19:703–708

Wang KH, McSorley R, Marshall A, Gallaher RN (2006) Influence of organic Crotalaria juncea hay and ammonium nitrate fertilizers on soil nematode communities. Appl Soil Ecol 31:186–198

Wardle DA, Yeates GW, Watson RN, Nicholson KS (1995) The detritus food web and the diversity of soil fauna as indicators of disturbance regimes in agro-ecosystems. Plant Soil 170:35–43

Wardle DA, Yeates GW, Williamson W, Bonner K (2003) The response of a three trophic level soil food web to the identity and diversity of plant species and functional groups. Oikos 102:45–56

Waring SA, Bremner JM (1964) Ammonium production in soil under waterlogged conditions as index of nitrogen availability. Nature 201:951–952

Yeates GW, Bongers T, de Goede RGM, Freckman DW, Georgieva SS (1993) Feeding habits in soil nematode families and genera- An outline for soil ecologists. J Nematol 25:315–331

Yeates GW, Bardgett RD, Cook R, Hobbs PJ, Bowling PJ, Potter JF (1997) Faunal and microbial diversity in three Welsh grassland soils under conventional and organic management regimes. J Appl Ecol 34:453–470

Zelenev VV, Berkelmans R, van Bruggen AHC, Bongers T, Semenov AM (2004) Daily changes in bacterial-feeding nematode populations oscillate with similar periods as bacterial populations after a nutrient impulse in soil. Appl Soil Ecol 26:93–106